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Laboratory Studies on House Fly Populations

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III. The Influence of Insecticides on Population Trends

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Bulletin 631
March 1960

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION
NEW HAVEN

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ACKNOWLEDGMENTS

This work was supported in part by a grant from the National Science Foundation. The technical assistance of Mrs. Eugenia Grabicki is gratefully acknowledged.

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III. The Influence of Insecticides on Population Trends

As part of a continuing study of the long-range effects of insecticides on house fly populations, insecticides are here considered in their ecological role. Various considerations bear on this outlook and suggest the experimental approach.

In the life of an insect, the presence of an insecticide is an environmental hazard. The insect may avoid this hazard, passively by chance, or actively by its behavior. It may overcome the hazard by physiologically moderating the action of the chemical. Insects surviving exposure are not necessarily free from further consequences of the insecticide. A chemically stable insecticide, or one that changes to a more toxic compound, may be a continuing environmental hazard to which individual insects are exposed repeatedly or continuously or to which different insects, coming and going, are occasionally subjected. An unstable insecticide, unless it becomes more toxic, may be a hazard for a short time in the life of an individual insect. Its hazard to an insect population may depend upon the proportion of the population present at the time of application. Because of differences in physical and chemical properties, insecticides and their formulations present different kinds and degrees of hazards to the insect population living in an already complex environment. Against these hazards the insects have adaptive potentialities stemming from gene-controlled differences in susceptibility.

It is of little moment whether an individual insect dies of old age, starvation, low temperature, or is killed by a parasite or an insecticide. The fate of an aggregation of insects on the other hand, may differ considerably depending upon how and at what time its individual members are killed.

The purpose of practical insect control by chemicals is to free or protect an area from insect pests. This occasionally may involve a contained insect population; more often, treatment is directed against a segment of a larger population, the size of which cannot be known. Under such field conditions, studies on insect control and its consequences are complicated by innumerable interacting forces that are difficult or impossible to evaluate. In contrast, most laboratory studies of insecticidal effects are made of confined insects regulated as to number and degree of exposure. Whatever the reason, laboratory studies often do not agree with field observations.

Classical laboratory studies of insect populations have shown that the killing of many insects may, in certain instances, favor larger numbers in succeeding generations by relieving competition at an appropriate time (e.g. Nicholson, 1954). But an insecticidal action may not be limited to a lethal effect; it may also modify the physiology of the survivors, possibly changing their powers of

reproduction (Knutsen, 1959). Development of resistance to insecticides has almost become the accepted pattern associated with the widespread and long continued use of insecticides. But this pattern differs widely among insecticides, species of insects, and ecological situations. Although many genetic and physiologic aspects of resistance seem to be understood, generalizations cannot be made without many qualifications. Also satisfactory means of avoiding the development of resistance or of overcoming resistance once it has developed have not resulted from the many studies on the problem. It is clear that insecticides as selecting or segregating mechanisms are not yet completely understood, and much can still be learned as to the conditions that favor this selective action. The normal fluctuations in insect numbers associated with life cycles and the normal variation in numbers imposed by limiting factors in the environment must influence, and in turn be influenced by, the role of insecticides as controlling agents.

Such diverse considerations point to the importance of observing continued insecticide treatments on populations of houseflies reared in the laboratory, but in situations where behavior is given opportunity for expression and where the flies themselves may modify the environment. Thus elements of both field and laboratory environments are combined in the technique employed here. Because so many different views are held by students of insect populations, some early experiments were necessarily designed "to see what happens." These are prerequisite to using the technique for testing hypotheses on the changes in fly biology induced by insecticides.

The question being asked here is essentially this: Aside from the suppressive action that is generally taken for granted, and the possible development of resistance by the insect, does the continued use of insecticides modify trends in house fly populations? Posing the question this way introduces a conflict of purpose when resistance does develop. Then comes a question as to whether the nature and extent of the resistance should be studied or whether the population should be controlled by effective chemicals and continued under observation. A chemically controlled population may show signs of modified physiology that can be studied only by sampling the population for separate rearing. But if the population is controlled at low levels, near extinction, it cannot be sampled without changing its character or even destroying it. Obviously experimentation can take many different courses, and some of the courses must be chosen expediently. This report is largely descriptive. A more critical appraisal of this technique applied to the resistance problem is reserved for the future.

Materials and Methods

Fly rearing conditions

The microcosm technique for rearing house flies continuously, as previously described (Beard, 1958), was used throughout these studies. Because chance mechanisms can operate in this system, it may be considered a stochastic model of population dynamics as discussed by Neyman and Scott (1959). The microcosm consists of twelve intercommunicating breeding sites arranged in three batteries of four units each. At the peak of emergence in each generation, the oldest battery is removed and fresh food and breeding media are added in a new battery, providing four fresh breeding sites.

The details of the rearing technique as described were modified only slightly as the experiment proceeded. A minor change was that the concentration of yeast used in the larval medium was reduced from a commercial package of dry yeast per liter of water to a measured 3.5 grams per liter, 50 ml. of which was added to 50 grams of dog food for each breeding unit. This amount proved adequate and is convenient and uniform.

At one stage it was found that the cotton dental rolls used as wicks for water were not so uniform as those formerly available. This occasionally resulted in an undesirable variation in fly distribution. The wick was consequently replaced by a sheet of absorbent unwoven cotton-rayon fabric fastened over the mouth of the water bottle by rubber tubing. This modification had the added advantage that evaporation was reduced without diminishing the availability of water to the flies.

A new and simpler device was adopted to measure fly activity. As was described, estimates of fly activity were made indirectly by judging the degree of soiling of papers placed in the flight compartments of the rearing units. These papers at first were evaluated by homogenizing them with a given amount of water, filtering the homogenate, and then testing the turbidity of the filtrate. This procedure was modified so that the optical density of the soiled paper itself was measured by a type of densitometer. A photographic enlarger was adapted to concentrate a light passing through the test paper onto the sensitive cell of a photometer. The optical density of the soiled paper is compared with the optical density of a clean paper, of the same kind and size, adjusted to zero. Thus a direct reading of the paper can be made very quickly. It should be appreciated that this measurement assesses indirectly the fly activity without permitting fine distinctions. No way has been found to calibrate the degree of paper soiling with actual numbers of flies present for definite periods of time — except with low numbers. The degree of soiling is not an arithmetic function of fly numbers. Under crowded conditions flies do not live so long, but are stimulated to greater activity than when few flies are present. Feeding activity and consequently regurgitation and defecation are different with different degrees of crowding. The composition of regurgitated fluids and feces must also vary with the conditions. Even though the soiled papers do not relate linearly to fly numbers, the general relationship of few flies-little soiling, many flies-much soiling holds true, and the optical density of soiled papers is a measure of this. The method is convenient and serves the purpose of evaluation as long as it is understood that the increment intervals are not necessarily the same and do not necessarily represent equal numbers of flies. The optical density measurement of soiled paper requires a scale of values which cannot be precisely calibrated in terms of turbidity values from paper homogenates. Consequently in the data presented in the next section, the indexes obtained by the newer method were adjusted by a factor that made the ranges of indexes coextensive in both methods.

Molds and mites are constant threats in a rearing situation such as is used. To guard against their becoming serious factors in reducing fly populations two devices were used. Tedion (*p*-chlorophenyl 2,4,5-trichlorophenyl sulfone) was added to the yeast-dog meal medium at a concentration of 100 p.p.m. Also a dry "mulch" was added to the top of the moist medium. This mulch was of buckwheat hulls dusted with Tedion, Aramite (2-(*p*-tert-butylphenoxy)-1-methylethyl 2-chloroethyl sulfite) and Tegosept (methyl ester of *p*-hydroxy-

benzoic acid). These chemicals were shaken in dry form with the dry hulls; the amounts adhering to the dry hulls cannot be expressed quantitatively. Although these precautions did not entirely eliminate molds and mites, they reduced these contaminants to inconsequential levels. An insect contaminant also appeared in the cultures. This was a small borborid fly (*Leptocera* sp., as identified by W. L. Downes, Jr.). Elimination of this fly from the cultures was impractical and unnecessary as it was essentially a scavenger. There was no evidence that it was competing with the house fly nor affecting the population trends either among the insecticidally treated or untreated series. Actually, these biological components added to the realism of the microcosm as a model system. Their presence would defeat the purpose of the experiment only if they or their interactions dominated other influences and overwhelmed the insecticidal effects.

Chemical treatment

It is axiomatic that to observe the long range effects of chemicals on insect populations, the populations must persist. This means that insecticidal control must not be complete. The survivors necessary to maintain a population can be of two types — those that survive a sublethal dose and those that luckily escape exposure. An early attempt was made to favor the first type by treating all sites of infestation, using dosages low enough to permit some survival. This proved impractical as the same dosage level at times exterminated the population and at other times gave inadequate control. The reason for this doubtless is that some groups of flies were exposed for a longer time than others, and this in turn was determined by a variety of factors. Alternatively, high dosages of insecticide were used, but not in all breeding sites. Sub-lethal doses were received by flies exposed to the chemical only briefly. Untreated breeding sites provided areas of escape. Although a predetermined method of application and dosage of insecticide was used as consistently as possible, complete objectivity was difficult. If mortality was excessive, treatment had to be relaxed somewhat to avoid terminating the series. If chemical treatment was inadequate to reduce fly numbers, the application of the insecticide was modified to secure better kill. These modifications contributed to major fluctuations in fly numbers, partly because they were made only in extreme cases. In other words, the corrective measures lagged behind the appearance of need for adjustment.

In all applications of pyrethrum, a 0.5 per cent solution of pyrethrins in kerosene was atomized as a space spray into the rearing units.

DDT and Dipterex (dimethyl (2,2,2-trichloro-1-hydroxymethyl) phosphonate) were initially incorporated in the dry food offered the adult flies, with DDT in 0.5 per cent and Dipterex in 0.1 per cent concentrations. Although these materials were highly effective when first presented, residual effectiveness was short-lived. This loss was not associated with development of resistance but was characteristic of this method of presentation. Later DDT was applied from acetone solutions as a heavy deposit to glass slides which were then placed in the rearing units. Dipterex was later presented in a sugar bait separate from the usual adult food source. Still later it was given more effectively in the water supply. Inasmuch as the time of exposure was not controlled, the actual concentration of the toxicant was not important so long as it was high enough to cause high mortalities at least initially.

The three toxicants, DDT, Dipterex, and pyrethrum were chosen to reduce fly numbers at three stages in the breeding cycle. Pyrethrum was applied to kill flies when they emerged in their rearing units, before they migrated to new breeding sites. Dipterex was applied primarily to reduce fly numbers as they invaded new breeding areas. DDT, because of its residual action, was assumed to reduce fly numbers effectively both as they emerged from breeding areas and as they invaded new sites. This assumption was not justified, as the residual action decreased too rapidly.

Modifications of the experimental design were made for special purposes. These will be discussed when appropriate.

Results and Discussion

Untreated series

The trends of untreated populations of flies are illustrated in Figures 1 and 2 (see also Beard, 1958). Figure 1 represents 45 food cycles (generations) of flies, all stemming from an original strain of flies obtained from the Quartermaster Research & Development Center, Natick, Massachusetts. Figure 2 covers the same period of time, but at the 16th cycle, flies obtained from the Boyce-Thompson Institute, and at the 34th cycle, flies from Rutgers University, were introduced to broaden the genetic spectrum. The fly traffic in both series fluctuated at generally high levels. The fluctuations are not apparently cyclic, nor can the extremes be assigned to any specific agent or condition. Even the conspicuously low level in the series represented in Figure 2 at cycles 35, 36, 37, and 38 cannot be attributed to any single factor. Although these follow the introduction of outside flies, it is unlikely that these flies were responsible for the subsequent low numbers. Other unexplained low populations where new flies were not introduced, and other companion series where new flies were introduced without consequent decreases in populations have been observed. In Figure 1 no obvious inbreeding effects are evident, and in Figure 2 no obvious advantages of outbreeding under the existing conditions appear.

DDT treatment

Figure 3 represents a series in which three of the four rearing units received DDT. A definite reduction in fly traffic is evident. A trend toward in-

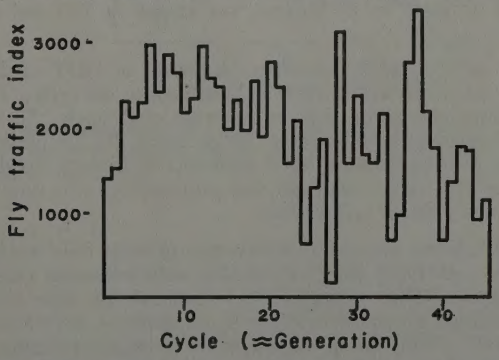


Figure 1. Fly traffic indexes for 45 cycles shown by one strain of flies reared without insecticides.

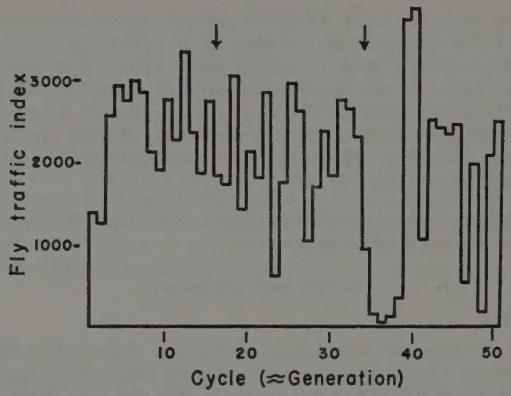


Figure 2. Fly traffic indexes for 50 cycles shown by one strain of flies augmented by another strain of flies at the 16th cycle and by a third strain at the 34th cycle (as indicated by arrows).

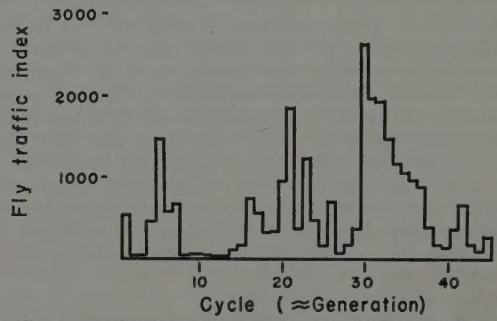


Figure 3. Traffic indexes for flies treated with DDT in 3/4 breeding sites for 29 cycles, the dosage being doubled at the 22nd cycle. Treatment was withheld in cycles 30 to 36. Lindane was applied in 37th and subsequent cycles.

creased traffic was reversed by doubling the dosage of DDT in the 22nd cycle. No treatment was made in the 30th and succeeding six cycles. In the absence of insecticide, the population did not increase explosively. To be sure there was a general increase to within normal range, but it did not persist. This is one of several cases pointing to a modified reproductive biology disadvantageous to the flies. At the 37th cycle, treatment was resumed but this time with lindane, and fly traffic was reduced still further.

Figure 4 illustrates a series in which two of each four rearing units were similarly treated with DDT for 29 cycles, but with treatment suspended for the following 13 cycles. Then treatment was resumed for four cycles. The first portion of this graph shows what might be expected — after a period of more or less successful control, the development of resistance permitted populations to return to normal levels. The curious pattern after the 30th cycle invites the tempting explanation that the flies went beyond the resistance stage and de-

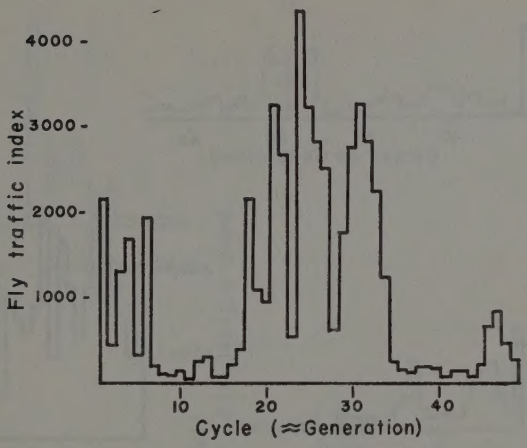


Figure 4. Traffic indexes for flies treated with DDT in 2/4 breeding sites for 29 cycles. Treatment withheld for succeeding 13 cycles, then resumed.

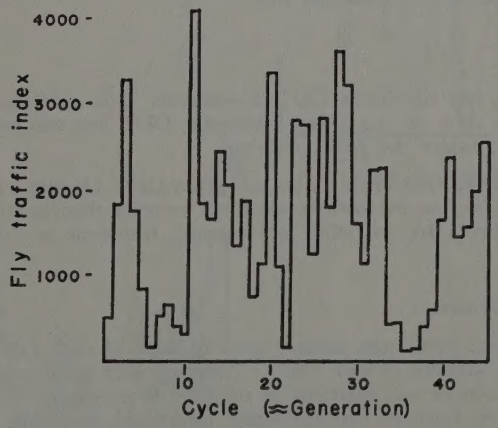


Figure 5. Traffic indexes for flies treated with DDT in 1/4 breeding sites for 29 cycles. Treatment discontinued in 30th cycle, but continued again with lindane in the 34th cycle.

veloped a DDT requirement so that when DDT was withdrawn, the fly numbers declined to marginal levels. Then when DDT was restored, thus providing a "requirement," the population picked up again. This is not an impossibility, but in this instance if there is any DDT dependence, it is more subtle. When these flies were sampled and reared simultaneously with and without DDT, those flies without DDT developed in noticeably, but not phenomenally, larger numbers. This difference held for four generations, dispelling any likelihood

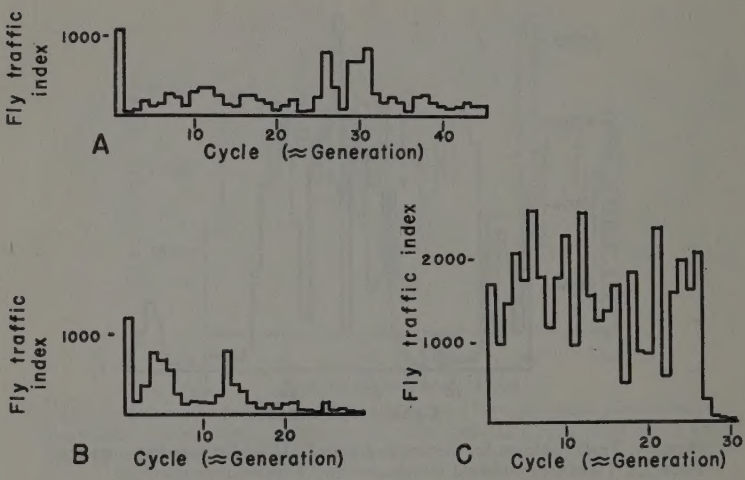


Figure 6. Traffic indexes for flies treated with pyrethrum in 3/4 (A), 2/4 (B), and 1/4 (C) breeding sites.

of there being any significant DDT dependence. This difference likewise indicated that in spite of (accepted) resistance, DDT was still exercising a depressive action under the test conditions.

When only one out of four sites was given DDT (Figure 5), no sustained control is evident, but fluctuations are more extreme than in untreated populations. This being so, the effect of stopping treatment at cycle 30 is not evident.

Pyrethrum treatment

In the three pyrethrum series, Figure 6, three of each four (A), two of each four (B), and one of each four (C) rearing units were sprayed. A certain amount of judgment was exercised as to time of treatment. When flies were at especially low levels so that extinction threatened, treatment was withheld. Otherwise the designated units were sprayed when flies were present. This might be daily if fly emergence was continuous; otherwise as needed. Except in special cases, flies invading a new site were not sprayed, but their emerging progeny were. It is apparent that comparatively consistent control was obtained when two or three of each four rearing units were sprayed, but control was not impressive when only one of the four was treated. All three series were terminated unintentionally when fly numbers became too low to survive. The proximate cause of the final decline is not known. Each failed at a different time and with no obvious association with external factors. No evidence whatever indicated any increased resistance to pyrethrum. On the contrary, all these three and two other series of fly populations treated with pyrethrum ultimately failed biologically.

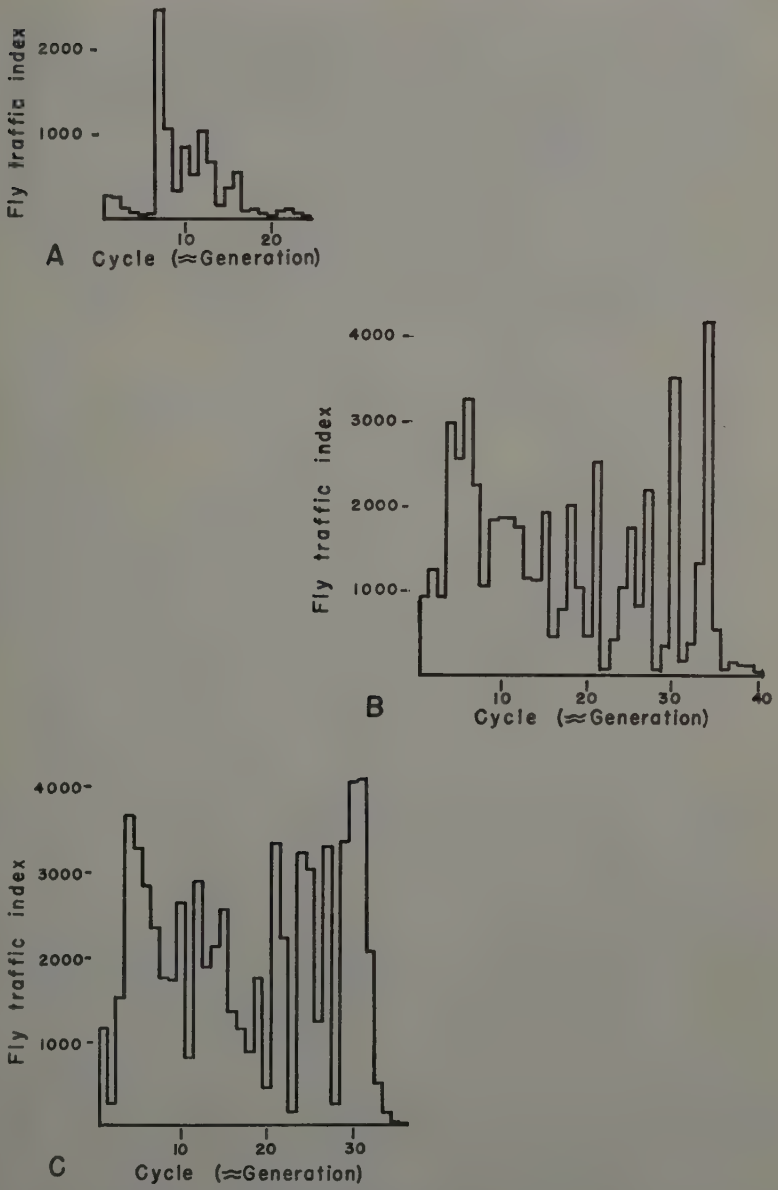


Figure 7. Traffic indexes for flies treated with Dipterex in 3/4 (A), 2/4 (B), and 1/4 (C) breeding sites.

Dipterex treatment

Figure 7 (A, B, C) illustrates the fly traffic patterns in populations given Dipterex in three, two and one of each four rearing units. The presentation of Dipterex was not entirely satisfactory, so control was not as effective as is possible with Dipterex. The Dipterex was mixed as an alcoholic solution with powdered milk and sugar and dried to yield a 0.1 per cent concentration. Contrary to general experience, this formulation was not effective for the duration of the "migration" to new breeding areas, so only the first migrants succumbed to the poison. Nevertheless these series permit the conclusions that (1) incomplete control promotes wide fluctuations in fly numbers from generation to generation (as seen also in Figure 5, with DDT); (2) in spite of incomplete control, all three Dipterex series failed, as did the pyrethrum series; and (3) no evidence of increased resistance to Dipterex appeared.

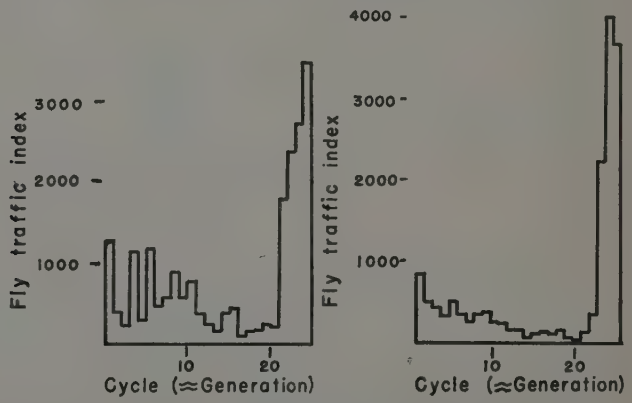


Figure 8. (Left) Traffic indexes for flies given limited food for 21 cycles, thereafter given full complement of food. Figure 9. (Right) Traffic indexes for flies given limited food and fewer breeding sites for 21 generations, thereafter given full complement of food and breeding sites.

Untreated series with limited food

On the basis that reduced breeding resources might produce the same results as chemical control, fly series were maintained with fewer breeding sites and limited larval and adult food. In the series represented by Figure 8, adult food was reduced to one-third and larval medium was reduced to two-fifths of that considered standard for the other breeding units. Clearly these food restrictions had a dramatic effect on the population. When the full complement of food was restored after 21 generations, a more "normal" level of population correspondingly resulted. If in addition to the food restriction just mentioned, larval food was completely omitted in two of each four units, the populations were limited still further (Figure 9). An even more striking recovery occurred when the food and breeding requirements were increased to the standard. In the series represented in Figure 10, complete adult food was supplied, and in two of the four units the standard larval medium was supplied. In the other two units moist sawdust was substituted; this, of course, does not support devel-

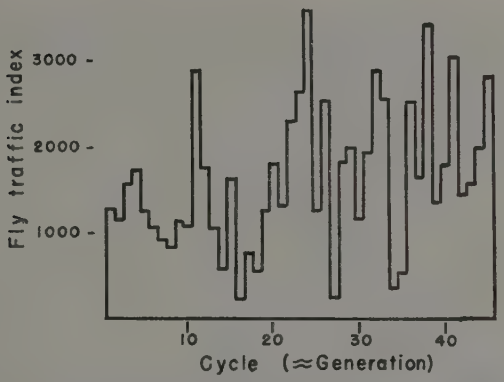
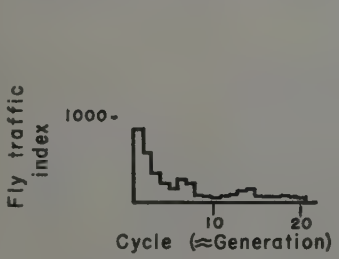


Figure 10. Traffic indexes for flies given fewer breeding sites and treated with DDT in 2/4 rearing units. After the 20th cycle breeding sites were restored.

opment. This reduction in breeding sites did not limit the populations as much as did the food restrictions, but a general rise in level is apparent after the twentieth cycle when the full number of breeding sites was restored.

In comparison with other series treated with insecticides, the significant feature of these series is that when the standard complement of food was introduced after a regimen of limited food, the populations promptly rose to levels which might be considered normal.



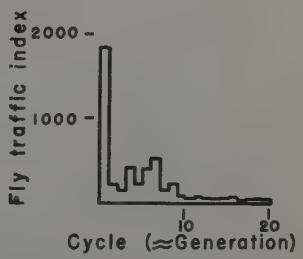


Figure 11. (Left) Traffic indexes for flies given limited food and treated with DDT in 2/4 rearing units. Figure 12. (Right) Traffic indexes for flies given limited food and treated with pyrethrum in 2/4 rearing units.

Treated series with limited food

The effect of insecticidal treatment superimposed upon restrictions in the environment was examined in one series treated with DDT and one treated with pyrethrum where food was limited as in those just mentioned. The insecticides were applied in two of each four units. Both adult and larval food were in short supply, but were present in all four units. The DDT series is represented in Figure 11 and the pyrethrum series in Figure 12. It is not surprising that low populations resulted, which ultimately dwindled to extinction. Both series were lost before the standard food supply was restored. In a com-

panion series with short food supplies (Figure 13) one of each four breeding units was treated with pyrethrum for 17 generations. Then treatment was stopped and the usual complement of food was provided. The population increased promptly, but the recovery was no more remarkable than with the untreated populations following restoration of standard food.

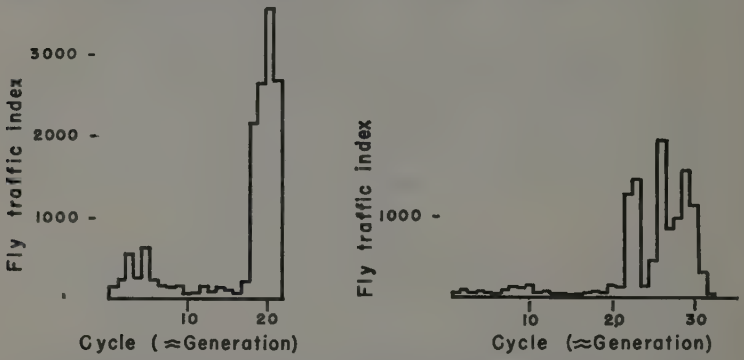


Figure 13. (Left) Traffic indexes for flies given limited food and treated with pyrethrum in 1/4 units for 17 cycles; thereafter given full complement of food and no pyrethrum treatment. Figure 14. (Right) Traffic indexes for flies given limited food and treated with DDT in 1/4 units for 17 cycles; thereafter given full complement of food and no DDT treatment.

The series illustrated in Figure 14 was similarly treated with DDT in one of four units for 17 cycles with restricted food; then food was restored to standard, and treatment was discontinued. Here the recovery was incomplete and the series failed completely after the 32nd cycle.

The food limitation in these several series was so severe that the added hazard of insecticides is difficult to evaluate. That the treated populations were marginal is evident, as the series illustrated in Figures 10 and 11 could not maintain themselves. Sampling these populations for biological study would have terminated the series, but it would have been interesting to evaluate these flies for susceptibility to the test chemicals. It is obvious, however, that any resistance that may have developed was not of sufficient advantage to favor larger populations or even survival.

Dispersal effects on trends of untreated populations

Since the earlier report (Beard, 1958) on the trends of fly numbers in the absence of insecticides, certain behavioral patterns associated with the rearing method have become apparent. These bear on interpretation of normal trends and on the direct and indirect effects of applied insecticides.

Peculiar situations develop with either especially large numbers or especially small numbers of flies. As many as fourteen hundred flies have developed in a single rearing unit, but only a few hundred flies create crowded conditions. When flies are crowded, their activity is stimulated and food is rapidly consumed. Thus situated, flies disperse if they can. This dispersal is probably much at random, but it is opportunistic. Flies tend to accumulate where they find

improved conditions, with more food and space. Elsewhere dispersal continues, probably until some kind of equilibrium is established. Thus, if new breeding sites are presented when flies are crowded, the dispersal pressure induces large numbers of flies to populate the new sites. The new sites then become crowded, the adult food is largely consumed, and the next generation is deprived of food unless it, too, can disperse to new areas. In a new area the crowded flies presumably lay an excessive number of eggs unless short rations have reduced their fertility. As a consequence, larval competition may also be severe, and the population may drop or the flies may be unusually small.

Another situation similar in result but different in form may arise from excessive numbers of flies. If presentation of new sites is delayed, dispersal does not relieve the crowding of flies emerging in large numbers within a short time. Lack of space, shortage of food, excessive activity, and accumulation of moisture and metabolic products contribute to unusually high adult mortalities. Then when new breeding sites are presented, few flies are physically able to migrate, and competition among their larval offspring is not severe. The next generation of flies may be small or moderate in number, but the individuals are usually large in size.

In contrast, flies in low populations behave differently, and their numbers may stay low simply because of their behavior. With adequate food in all areas and little stimulus for activity, dispersal pressure is low. New breeding sites when presented are not necessarily attractive to flies at a distance. Hence they may not become occupied promptly. If breeding media are no longer favorable where the flies are present, some reproductive potential may be wasted. Wilkes *et al.* (1948) observed that isolated flies do not deposit normal numbers of eggs. This condition, too, would tend to make small populations self-limiting.

The time when new breeding sites are presented would be unimportant if the breeding material was at all times the same. But the medium changes physically, chemically, and biologically, and so must vary in its attractiveness and suitability as a breeding medium. It has been found acceptible to flies for at least twelve days and may even support a second generation under favorable conditions as when the first generation has not exhausted the nutrients. The changes occurring in the absence of flies result largely from the growth of yeasts, bacteria, and mold. Some of these are favorable, others unfavorable, for fly development. Fermentation is probably most active a day or two after the medium is prepared. The breeding containers were designed to minimize moisture changes, but with a tendency for desiccation in unoccupied units on one hand and the addition of metabolic moisture in occupied units on the other, this factor cannot be controlled. This being so, the time of setting new breeding areas could be important.

Correlation of life cycle with availability of new breeding sites

The presentation of new breeding sites when flies are emerging in greatest numbers seems feasible and logical. Accordingly this became standard practice in most of the experimental series. This has at least two possible disadvantages. One is that peak emergence must be judged by the untreated populations, and treated populations do not necessarily follow the same trend. The second is that the flies first to emerge are favored as they mature first and so are most likely to reproduce. With temperature controlled to some degree this program became somewhat regularized to replacements about every 16 or 17 days.

Alternatively new breeding sites could be added strictly on a regular time basis without regard to the life cycle. This was done in two series for comparison with the regular system. New breeding sites were added every two weeks to one series and every three weeks to the other. In both the two- and three-week series there would be times when the life cycle would be in phase and other times when it would be out of phase with the presentation of new media. Out-of-phase presentation might be expected to result in low populations unless relaxed competition counter-balanced any reduced nutrition. The trends of fly activity in series maintained on the three time schedules for a ten-month period are shown in Figure 15. These represent series maintained for the same ten-month period and started from the same stock of flies. Except for four obvious low points, the two-week cycle shows no more irregularity than the regular series. The four low points are sufficiently regular to suggest a phasic condition, but the presence of flies at all times tended to minimize the out-of-phase effects. The three-week cycle, however, shows greater fluctuations; the generally lower activities possibly reflect longer periods out of phase. The three-week schedule would more often than not favor flies with slower development. Thus, in view of the association of DDT resistance with slow fly development, the three-week cycle flies might develop resistance more rapidly than the two-week cycle flies. For this reason, lindane was applied to two series, one on a two-week cycle, and the other on a three-week cycle. In both series two of each four units received lindane as deposits on glass slides. A third, standard, series treated with lindane was available for comparison. From Figure 16 it is evident that whereas lindane initially kept the population low for more cycles in the two-week series (A)

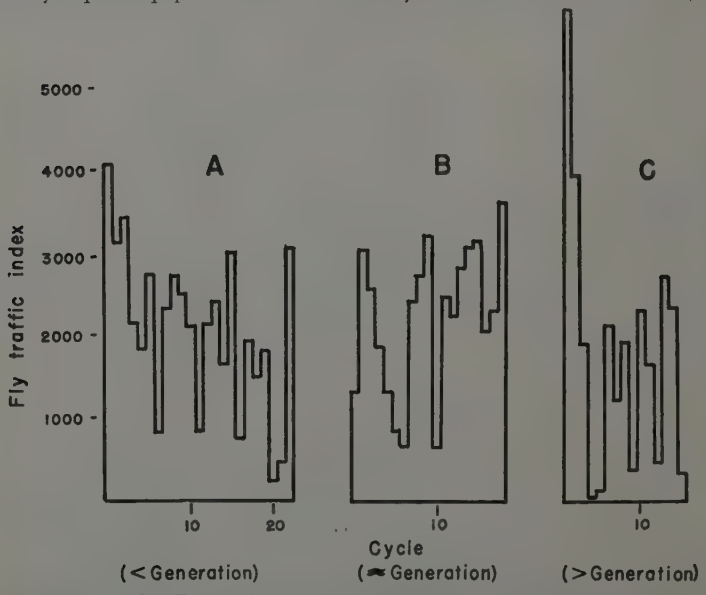


Figure 15. (A) Fly traffic indexes for 22 cycles on a two-week basis. (B) Indexes for 18 cycles on a fly generation basis. (C) Indexes for 15 cycles on a three-week basis. All cover the same time period.

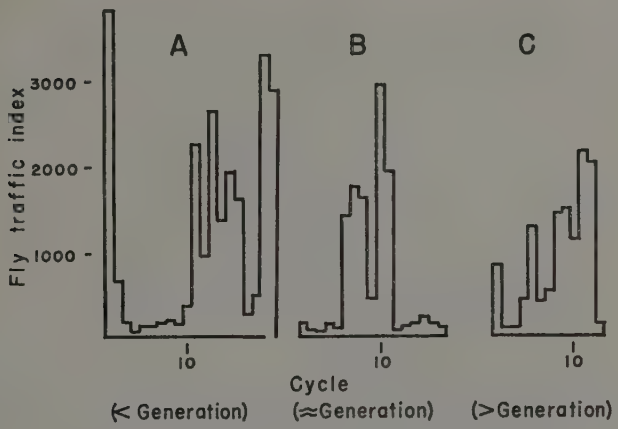


Figure 16. A, B, C. Fly traffic indexes for cycles similar to those in Figure 15, but in each series 2/4 rearing units were treated with lindane.

than the three-week series (C), the fly traffic index later rose to high levels. It is possible that in this series selection occurred for shorter life cycles so there might have been in fact more generations as well as more cycles. The standard series (B) is not strictly comparable with the other two, as treatment was not consistent with them. Lindane was withheld at the tenth and eleventh cycles. This accounts for the two highest values. The population dropped, however, in the twelfth and succeeding cycles when lindane treatment was restored in three, rather than two, of the four units. A suggested resistance was thus apparently overcome by more complete treatment.

An evaluation of resistance by topical application of acetone solutions of lindane to flies of the two-week cycle after 15 cycles and to flies of the three-week cycle after nine cycles indicated similar degrees of resistance — both groups requiring dosages about 40 fold those for equivalent mortalities in susceptible flies. Thus, if there was an early more rapid increase in resistance in flies of the three-week cycle the difference was not maintained.

Dispersal effects on trends of treated populations

Trapping Action of Insecticides

Fly movement from unit to unit in the system may be modified by the presence of insecticides. An effective insecticide, present at all times, may trap most of the flies. If each fly in a treated unit gets a fatal dose and dies quickly, it remains there. Flies randomly migrate from other units. These flies in turn die. The treated units therefore can have large numbers of dead flies whereas the untreated units contain no flies, living or dead. This gives the appearance of attraction by the treated units and fly traffic indexes may show curious reversals. Although attraction is possible, random movement and the rapid killing action of the insecticide adequately explain this behavior. This phenomenon need not result in extermination of the flies if adequate oviposition has occurred prior to complete mortality. Nevertheless extermination in such a closed system is possible and is independent of population size. This was dramatically illustrated in a

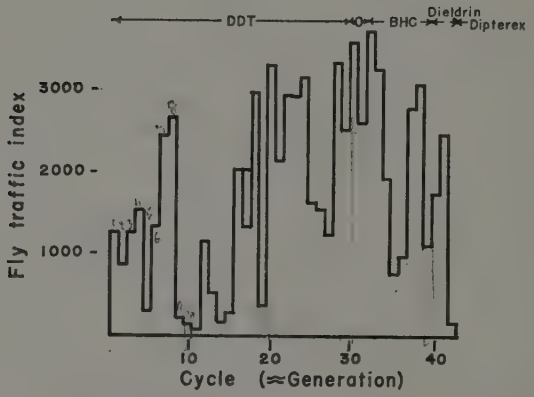


Figure 17. Traffic indexes for flies treated with DDT in 2/4 units for 30 cycles, untreated for 2 cycles then treated with lindane for 7 cycles and dieldrin for 3 cycles. In the 42nd cycle Dipterex exterminated the series.

series (Figure 17) treated 30 generations with DDT. As resistance developed, DDT failed to control the population. Lindane was substituted in the 33rd and subsequent six cycles, but the flies were not susceptible to this. This represents an almost unique case of DDT-lindane cross-resistance. At least it is contrary to the generalization (Brown 1958) that DDT resistance does not confer resistance to lindane in the housefly even though it may in *Drosophila.* Neither were the flies susceptible to dieldrin which was applied during cycles 40, 41, and 42. In other words, the flies resistant to DDT were also resistant to lindane and dieldrin. But when Dipterex was added to the water supply in three of the four units, all flies died without issue. The area of escape provided is effective only if the flies take advantage of it, spending sufficient time there to reproduce. In this case, the trapping action of the Dipterex created one-way migration, leaving the area of escape barren.

Equalizing effects of dispersal

The trapping action just described is unusual, made possible only by random dispersal and the prompt, completely lethal action of the insecticide. More often, the dispersal tends to equalize the populations in the four units of each battery. This dispersal has already been reported for untreated populations where certain breeding units were omitted (Beard 1958). Table 1 indicates the mean fly-traffic indexes in treated and untreated units of nine series each covering about 45 cycles. An analysis of variance is not needed to point out two conclusions, (1) that treatment as made in these series reduces but does not "control" locally the fly populations nor does it "protect" the treated units, principally because the flies migrate from unit to unit, and (2) that, as would be expected, the more units treated, the greater is the general reduction in the confined populations.

Table 1. Mean fly-traffic indexes in units of nine series

131	*97*	*72*	*63*	
256	170	*138*	*131*	DDT
365	450	487	*248*	
75	*66*	*43*	*41*	
131	95	*63*	*47*	Pyrethrum
437	425	480	*186*	
100	*188*	*85*	*84*	
432	350	*432*	*364*	Dipterex
540	520	398	*398*	

Italic figures = values from treated units

A comparison of these data with those previously reported for series with reduced breeding sites (Table 2, Beard 1958) indicates that the disparity in fly activity between sites with and without larval food (breeding media) is greater than that between sites untreated and treated with insecticides. In other words, dispersal is greater when insecticides are the population deterrent than when breeding sites are unfavorable, even though total activity is less in the treated series.

Concluding Comments

Several generalizations emerge from the observations reported. Although they apply strictly to the conditions of test, they may have much broader application.

The fluctuations in the trends of untreated populations, even those reaching extreme values, need no particular explanation. Although the extreme values might reflect specific causal mechanisms or situations, the random combination of independent factors could by chance result in abnormally low or abnormally high population levels, as suggested by the studies of Cole (1958) and Schwerdtfeger (1958). Either with or without insecticidal treatment none of the series shows cyclic fluctuations that might be introduced by internal regulating mechanisms as found by Nicholson (1954).

It may be that the less complicated patterns seen in the Dipterex and pyrethrum series is evidence that the actions of these chemicals is predominantly primary, with few or no secondary actions or side effects. If so, they may do little more than randomly remove an unspecialized portion of the flies. On the other hand DDT and similar type insecticides may not be limited to primary actions and more selectively remove flies to leave more specialized individuals with greater genetic survival value with respect to the chemicals used.

Population behavior (as distinct from individual behavior) seems more responsive to changes in food and breeding situations then to the influence of insecticides. This is to say that fly numbers are more directly related to the abundance and scarcity of food and breeding media than they are to the presence or absence of insecticides. This conclusion is based on the severe effect of limited food, the prompt recovery in numbers when adequate food is supplied, and the differences in dispersal under different conditions.

The less direct, but none the less important, population response to changes in insecticidal treatment is manifested in several ways.

To be sure, the introduction of a killing agent into a susceptible population can promptly reduce numbers dramatically. As an extreme case, the complete loss of a series by the trapping action of Dipterex can be cited. But in all other series observed, the insecticidal effect was less definite, ranging on down to inducing wide fluctuations in fly numbers without appreciably reducing the mean population size.

Apart from the direct killing action of the insecticides, indirect actions on the biology of the fly populations are clearly evident. These are subtle and difficult to define, but they differ with different insecticides and with the time and manner of application. The ultimate failure of the pyrethrum series and the Dipterex series, even when treatment was withdrawn, indicates less resilient populations than when populations are kept low by food shortages. The development of resistance to DDT with cross-resistance to other insecticides, represent expected biological change. The fact that resistant populations do not necessarily build up to the carrying capacity of the environment is another example of reduced reproductive powers resulting from prolonged use of insecticides. This phenomenon and also increased reproductive powers have been reported by several workers who are cited by Knutsen (1959).

The various population patterns testify that the several insecticides differ in their long range effects, and their influence is not limited to their lethal action in merely removing a portion of the flies. Most of this influence is doubtless in the nature of selection for biological factors, some favorable, some deleterious. But the possiblity of chronic effects or induced changes cannot be entirely dismissed.

It was thought that these studies might show differences in populations attributable to the stage in life cycle most influenced by the killing agent or to the manner of presenting the chemical. These and other factors are confounded, however, and a different set of comparisons are required to clarify these points.

The reported observations permit this conclusion in terms of the objectives of the study: long-range effects of insecticides exist, but they are subtle, and except for the development of resistance to insecticides, the effects tend to be unfavorable to fly populations. The practical problem of higher populations associated with continued use of insecticides seems to be narrowed to the development of resistance to the insecticides. The biological changes that might account for lower populations following the use of insecticides, sometimes in spite of resistance, raise important questions of practical significance yet to be answered.

Summary

As a further report on studies of house fly populations reared in specialized laboratory environments, this bulletin considers insecticides as ecological factors affecting insect numbers.

By a microcosm technique already described, house flies were reared for up to 45 generations while exposed to different insecticides. Populations subjected in different degrees to DDT, Dipterex, or pyrethrum are compared with untreated series. The population levels reflect the effectiveness of the chemical as an environmental hazard and demonstrate differences in biological response to the different insecticides. The suppressive action of the insecticides did not necessarily stop when treatment was discontinued, thus indicating behavioral or physiological changes in the flies. Certain series failed in spite of resistance to DDT, which commonly developed under the test conditions. An unusual cross-resistance to lindane appeared, and resistance to dieldrin quickly succeeded resistance to DDT.

Flies maintained at marginally low levels by severely limiting their food and breeding resources, increased promptly to usual numbers when full complements of these resources were supplied. In this respect these populations were much more resilient than populations suppressed by insecticides for many generations and then reared in the absence of insecticides.

Consideration was given to the synchronization of life cycle with respect to the availability of breeding resources as possibly influencing the development of resistance. The results of these observations were inconclusive.

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